RESEARCH ARTICLE

Scaling Relations of Length-Biomass Allometry for Bi-dimensional Macroalgae: A Simple Theoretical Explanation

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ABSTRACT: A scaling exponent of 0.472 was obtained from some experimental observations of bi-dimensional seaweeds for their length-biomass allometry. It was sufficiently higher than the value of 0.25, which was almost regarded as the universal exponent, on the basis of the experimental data obtained for unicellular microalgae and vascular plants. Later, a simple theoretical model predicted a length-biomass exponent of 0.5, which was consistent, to a certain extent, with the data for bi-dimensional seaweeds. The present article has a theoretical study based on an assumption of a power-law relation existing between the two length parameters of a bi-dimensional organism, upon which the scaling exponent has been found to depend. The length-biomass scaling exponents can be expressed in terms of its power index. Mathematical expressions of biomass, of a bi-dimensional organism, in terms of its two length parameters, have been formulated here, which would be useful for experimental studies on allometric scaling. A theoretical model has been proposed to explain the origin of the scaling exponent of 0.25, observed for vascular plants. An attempt has been made to extend this model for two dimensional species, to three dimensional species, by assuming the existence of allometric relations among the length parameters along three mutually perpendicular directions.

KEYWORDS: Allometric Scaling, Length-biomass Allometry, Bi-dimensional Seaweeds, Macroalgae, Mathematical Biology.

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1. INTRODUCTION

It is widely observed in the biological domain that a variable (say Y), representing a biological quantity, has a power-law dependence on mass (M), expressed as $Y = aM^b$ where a and b are constant parameters. This power-law dependence on mass is called allometric scaling of the quantity (Y) where a is a constant of proportionality and b is known as the allometric scaling exponent.

According to Niklas and Enquist, there is a mathematical relation which is regarded as the universal scaling law for primary producers [1]. This law is expressed as,

$$L \propto M^{0.25} \qquad (1)$$

In equation (1), L denotes the body length which has an allometric dependence upon the mass M, showing a scaling exponent of 1/4 or 0.25. But this expression, regarded as *universal* for primary producers, was obtained by an analysis of experimental data for vascular plants, unicellular microalgae and a single macroalgal species (*Macrocystis*, Laminariales).

To test the validity of equation (1) for macroalgae, a researcher, named Scrosati, studied four phylogenetically distinct seaweed species: *Chondrus Crispus* Stackhouse, *Pterocladiella capillacea* (Gmelin) Santelices and Hommersand, *Fucus vesiculosus* Linnaeus and *Laminaria saccharina* (Linnaeus) J.V. Lamouroux [2]. On the basis of these experimental observations, the following scaling law was proposed.

$$L = 7.811\, M^{0.472} \qquad (2)$$

The species, studied by Scrosati, are of predominantly flat (bi-dimensional) seaweeds representing two orders of the Rhodophyta (red algae) and two orders of the Phaeophyceae (brown algae) [2]. Their configurations are likely to change with water flow but they are essentially flat when pressed on a surface [3].

The scaling exponent value of 1/4 or 0.25, proposed by Niklas and Enquist, was originally obtained for the length-biomass relation between the height and mass of a tree [4]. The theoretical foundation of this relation was in another law, according to which, the metabolic rate has an allometric dependence on an organism's biomass, showing a scaling exponent of 3/4 or 0.75 [5]. It was later found that no single scaling rule was appropriate for all species of vascular plants [6].

Using simple geometrical procedures, a researcher, named Ji-Huan He, provided a theoretical interpretation of Scrosati's findings [7]. The species, studied by Scrosati, are almost flat and they are found to grow in two dimensions (say *length* and *breadth/width*). The third dimension, i.e. the thickness, is not found to change appreciably with time. Thus, the mass is directly

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proportional to the surface area which is generally regarded as proportional to the square of any length parameter. Considering this bi-dimensional nature of growth, Ji-Huan He has shown the mass to be proportional to the square of length along any direction. Therefore we have,

$$L \propto M^{1/2} \quad (3)$$

The allometric relation of equation (3) is sufficiently consistent with the most of Scrosati's findings for seaweeds [2]. This expression, derived by Ji-Huan He, must have been based on an assumption that the two growth dimensions (say *length* and *breadth/width*), of a bi-dimensional species, are proportional to each other. It is generally observed that the growth process does not take place at the same rate along these two dimensions. Therefore, the lengths along two mutually perpendicular directions should not be regarded as proportional to each other in any theoretical formulation to interpret the experimental findings. Using the theories of allometric scaling regarding the metabolism of a biological organism, researchers have mathematically devised some methods to determine the time variation of any of these length parameters and also the time evolution of biomass (M) [8 - 10].

In the present article we have provided a theoretical explanation for the scaling exponent (i.e. 0.472) shown by equation (2), expressing the allometric relation that represents Scrosati's observations regarding bi-dimensional seaweeds [2]. For this purpose we have assumed a power-law relation to exist between two mutually perpendicular growth dimensions (say *length* and *breadth/width*), having different power indices for different species. There can be a special case where these two length parameters are proportional to each other, causing the power index to be unity. We have also formulated a theoretical model to explain the allometric relation of equation (1). We have extended our model for bi-dimensional species to those showing the growth process in three dimensions.

2. MATHEMATICAL ANALYSIS

For an organism undergoing a three dimensional growth process, it would be possible to find three mutually perpendicular directions along which its lengths change with time. In order to measure the size of a bi-dimensional seaweed we may choose two mutually perpendicular directions along which the growth takes place in that organism. Generally the growth process does not take place along these two directions identically. To determine the volume of such an organism, one should measure two length parameters (L_1 and L_2, say), which are functions of time, and the constant thickness (h). Irrespective of its shape, one can determine the size of the smallest rectangle in which it can be accommodated. The sides of such a rectangle can be the length parameters denoted by L_1 and L_2.

2.1 *Bi-dimensional Seaweeds*

Since L_1 and L_2 are quite likely to have different allometric relations with mass, it would be natural to consider a power-law relation between L_1 and L_2, as represented by the following equation.

$$L_1 \propto (L_2)^{\beta} \quad (4)$$

In equation (4), the power index β depends on the mechanism of biological processes occurring within the organism. When L_1 is proportional to L_2, we have $\beta = 1$.

Assuming uniform density of the body, the mass can be expressed in the following way (using eqn. 4).

$$M \propto volume \propto L_1 L_2 h$$

$$\text{or, } M \propto (L_2)^{\beta} L_2 h \equiv h(L_2)^{1+\beta} \quad (5)$$

In the above relation, the thickness (h) is a constant for a flat structure. We therefore get the following relations connecting L_1 and L_2 to M.

$$L_1 \propto M^{\beta/(1+\beta)} \quad (6)$$

$$L_2 \propto M^{1/(1+\beta)} \quad (7)$$

According to equations (6) and (7), when $\log(M)$ is plotted graphically as a function of $\log(L_1)$ and $\log(L_2)$, one gets straight lines with slopes $(1+\beta)/\beta$ and $(1+\beta)$ respectively. Using experimental data one can determine the slope and calculate the value of β.

In the special case where L_1 and L_2 are proportional to each other, we have $\beta = 1$ and then, from equations (6) and (7), one gets,

$$L_1 \propto M^{1/2} \text{ and } L_2 \propto M^{1/2} \quad (8)$$

Equation (8) has exactly the form derived by Ji-Huan He from very simple geometrical considerations [7].

Equations (6) and (7) represent respectively the allometric dependence of the length parameters L_1 and L_2 upon mass (M). Here, the scaling exponents for L_1 and L_2 are $\beta/(1+\beta)$ and $1/(1+\beta)$ respectively.

Comparing equation (2) with equations (6) and (7) we get the following values respectively.

$$\frac{\beta}{1+\beta} = 0.472 \text{ or, } \beta = 0.8939 \quad (9)$$

$$\frac{1}{1+\beta} = 0.472 \text{ or, } \beta = 1.1186 \quad (10)$$

The above discussions have provided a theoretical interpretation of Scrosati's findings [2]. Scrosati found the exponent of length-biomass allometry, for flat

seaweeds, to be 0.472. This value is possible for L_1 if $\beta = 0.8939$ and it is possible for L_2 if $\beta = 1.1186$.
If $L_1{}^{/}$ and $M^{/}$ are the experimentally observed values of L_1 and M respectively, at any stages of growth, we can write (using eqn. 6),

$$\frac{L_1}{L_1{}^{/}} = \left(\frac{M}{M^{/}}\right)^{\beta/(1+\beta)} \quad (11)$$

If $L_2{}^{/}$ and $M^{/}$ are the experimentally observed values of L_2 and M respectively, at any stages of growth, we can write (using eqn. 7),

$$\frac{L_2}{L_2{}^{/}} = \left(\frac{M}{M^{/}}\right)^{1/(1+\beta)} \quad (12)$$

Equations (11) and (12) are the mathematical expressions connecting M to the length parameters L_1 and L_2 respectively. For experimental purposes, these equations can be useful in estimating the mass (M) from the length parameters at different stages of growth.

2.2 *Vascular Plants*

A vascular plant, or a part of it, may often be considered to have a cylindrical shape, constituted by a bundle of fibres or tubes acting as tissues conducting food and water for the plant. The length of the cylinder is the same as the length of each tube. Let a cylinder of length L has a bundle of n tubes of radius R. If n and R are assumed to be allometrically connected to L, through scaling exponents β_1 and β_2 respectively, we can write,

$$n \propto L^{\beta_1} \quad (13)$$

$$R \propto L^{\beta_2} \quad (14)$$

Using equations (13) and (14), the mass of the entire cylinder can be expressed as (assuming uniform density),

$$M \propto nLR^2 \propto L^{\beta_1} L L^{2\beta_2} \equiv L^{\beta_1+2\beta_2+1} \quad (15)$$

In the cases where $\beta_1 \approx \beta_2 \approx 1$, equation (15) leads to the following relation.

$$M \propto L^4 \text{ or, } L \propto M^{1/4} \quad (16)$$

The allometric dependence of length upon mass, expressed by equation (16), is the same as equation (1) which was proposed by Niklas and Enquist as the universal scaling law for primary producers [1]. In all possible cases where $\beta_1 + 2\beta_2 = 3$, we must obtain $L \propto M^{1/4}$ from equation (15).

2.3 *Three Dimensional Growth*

Let L_1, L_2 and L_3 be the three length parameters used to measure the growth of a three dimensional organism along three mutually perpendicular directions. Considering L_2 and L_3 to be allometrically dependent upon L_1, through the exponents γ_2 and γ_3 respectively, we can write,

$$L_2 \propto L_1{}^{\gamma_2} \quad (17)$$

$$L_3 \propto L_1{}^{\gamma_3} \quad (18)$$

Using equations (17) and (18), we get the following allometric relation between length and mass (assuming uniform density throughout the body).

$M \propto L_1 L_2 L_3 \propto L_1{}^{(1+\gamma_2+\gamma_3)}$ or,

$$L_1 \propto M^{1/(1+\gamma_2+\gamma_3)} \quad (19)$$

Using equations (17) and (18), the mass can also be expressed in terms of L_2 and L_3. The allometric relations obtained for them are given below.

$$L_2 \propto M^{\gamma_2/(1+\gamma_2+\gamma_3)} \quad (20)$$

$$L_3 \propto M^{\gamma_3/(1+\gamma_2+\gamma_3)} \quad (21)$$

Equations (19), (20) and (21) express the allometric dependence of the length parameters L_1, L_2 and L_3 respectively upon the biomass (M). These length parameters can be the three sides of the smallest rectangular parallelopiped that can accommodate an organism at any stage of its growth. As one plots the logarithm of M as a function of the logarithm of L_1 (or L_2 or L_3), one gets a straight line with a slope of $(1 + \gamma_2 + \gamma_3)$ (or $\frac{1+\gamma_2+\gamma_3}{\gamma_2}$ or $\frac{1+\gamma_2+\gamma_3}{\gamma_3}$). From the log-log plots of biomass versus length, based on experimental data, one can determine these slopes from which the values of the parameters γ_2 and γ_3 can be easily calculated. If the values of γ_2 and γ_3 are close to 1, the slope of the straight lines will be close to 3. In a recent study on shrimps in India, these values are found to be close to 2.96 [11].

In one of our previous studies on length-biomass allometry, we provided an explanation for the allometric exponent found for bi-dimensional seaweeds [12]. However, that theoretical formulation could not provide any explanation for the exponent of 1/4, obtained for vascular plants and regarded as the *universal* scaling exponent for primary producers [1]. The present article provides theoretical interpretations for both observations. It also provides us with an outline to derive mathematical models of allometric scaling for plants and animals showing three dimensional growths.

3. CONCLUSIONS

A simple mathematical model is proposed in the present article to interpret the scaling exponent for the length-biomass allometry of bi-dimensional seaweeds. According to the explanation provided by Ji-Huan He, the value of the scaling exponent should be 0.5 [7]. But this value was obtained from oversimplified geometrical considerations where two mutually perpendicular length parameters were taken to be proportional to each other during the entire process of growth. In the present study, we have proposed a theory which is based upon an assumption that each length parameter has its unique allometric dependence upon mass. It causes the two length parameters of a bi-dimensional organism to have a power-law relation between them. The power index (β) is found to play a significant role in the determination of the length-biomass scaling exponent. It has been clearly shown that the length-biomass scaling exponent of 0.472, obtained from Scrosati's study [2], is valid for L_1 (or L_2) if $\beta = 0.8939$ (or $\beta = 1.1186$). The parameter β can be experimentally measured for a few specimens of any species of a bi-dimensional organism, and the scaling exponent for length-biomass allometry, for that species, can be determined from its average value. Expressions of biomass (M), derived in the present model, in terms of L_1 and L_2, can be used for experimental studies on the species having bi-dimensional growth. A model has been proposed here to interpret the length-biomass allometric scaling exponent of $1/4$, obtained for vascular plants. For that purpose, a plant of that type has been considered to have a cylindrical structure, consisting of a collection of tiny cylinders, acting as tissues. In the last sub-section of mathematical analysis, our model of scaling for two dimensional organisms has been extended to three dimensions, by assuming three length parameters to have allometric scaling relations among one another. The mathematical models proposed by us, in the present study, are expected to be useful in experimental studies on length-biomass allometry for both plants and animals.

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